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A FOURTH NEW SAUROPOD DINOSAUR FROM THE UPPER JURASSIC OF THE COLORADO PLATEAU AND SAUROPOD BIPEDALISM

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ABSTRACT.—The new sauropod, *Cathetosaurus lewisi*, is named and assigned to the Camarasauridae; it was collected from the Upper Jurassic Morrison Formation in western Colorado in 1967. Novel structural features of the skeleton in this genus, particularly in the axial skeleton, enabled it to assume and function to an unknown degree in a bipedal posture. Comparisons are made between *C. lewisi* and previously described sauropods. The following problems of sauropod locomotion are discussed: (1) sauropods lack two elements, sesamoids and patella, present in titanotheres; (2) sauropod limb and foot musculature, lacking leverage, is very inferior to that of titanotheres; (3) no previously described sauropod displays adequate structural specializations for voluntary bipedalism comparable to that of the new genus *Cathetosaurus*; (4) great weight and cartilaginous limb and foot joint structure restricted sauropods to a slow tempo of locomotion, suggesting a moderate to low rate of catabolic metabolism. Mammal and sauropod foot bones and their function are compared, and comparisons are made between the weight and structure of modern mobile machines and the locomotion and movement of large sauropods. Occurrence and taphonomy of *C. lewisi* are discussed.

Three sauropod dinosaurs, *Ultrasaurus macintoshi*, a brachiosaurid, *Supersaurus vivianae*, a (?)diplodocid, and *Dystylosaurus edwini*, family indeterminate, were recently described (Jensen 1985) from the Uncompahgre fauna (Jensen 1985) of the Jurassic Morrison Formation on the Southwestern Colorado Plateau in western Colorado. Diagnostic elements of these sauropods were collected from Dry Mesa Quarry, above the mouth of Middle Fork of Escalante Creek, on the eastern Uncompahgre monocline. The articulated skeleton of a fourth new, North American Jurassic sauropod, also from the Uncompahgre fauna, is described here as *Cathetosaurus lewisi*, new genus, new species. It was collected in 1967 from Dominguez/Jones Quarry on the eastern monocline of the Uncompahgre Upward, near the confluence of Big and Little Dominguez creeks.

The basic novelty of this fourth new sauropod is seen in the structural specializa-

tions of its skeleton, which enabled it to elevate its preacetabular body and maintain a bipedal posture. No sauropod genus has been previously described with comparable structural features. I do not suggest that this new sauropod was capable of significant bipedal locomotion, as if reverting to the supposedly bipedal behavior of an ancestral prosauropod, but only that it could stand bipedally and possibly engage in limited activities, one of which may have been arboreal foraging.

SYSTEMATIC PALEONTOLOGY
Order Saurischia
Suborder Sauropodomorpha
Infraorder Sauropoda
Family Camarasauridae
Cathetosaurus lewisi n. gen., n. sp.

ETYMOLOGY.—Greek: *kathetos*, perpendicular, referring to an ability to stand erect on its rear legs; *sauros*, lizard. Specific name *lewisi*, honoring Mr. Arnold D. Lewis, stout

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companion of the trail, who patiently trained me in laboratory and field work.

HOLOTYPE.—BYU 9740, an articulated sauropod skeleton including; atlas/axis plus 12 cervical vertebrae with ribs; right humerus, radius, ulna, and partial manus; 12 dorsal vertebrae, 1 dorsosacral vertebra; 20 dorsal ribs; 4 sacral vertebrae, and ribs co-ossified with 1 ilium; 1 pubis; both ischia; 43 anterior caudal vertebrae with many articulated chevrons.

TYPE LOCALITY.—Dominguez-Jones Quarry, Pit 1, above confluence of Big and Little Dominguez creeks; T14S, R9SW, New Mexico Principal Meridian, Mesa County, Colorado.

HORIZON.—Approximately 10 m above the base of the Brushy Basin Member, Morrison Formation, Upper Jurassic Period.

COLLECTOR.—James A. Jensen, 1967.

DIAGNOSIS.—All cervical neural spines bifid except atlas/axis; prominent pre-epipophyseal ridges, not reported in any other sauropod, present on superior surfaces of all cervical postzygapophyses; suprapostzygapophyseal laminae on cervical vertebrae not aligned nor confluent with epipophyses, as in all other sauropods; all dorsal spines bifid except last dorsal; pelvis with anterior iliac processes rotated ventrally around transverse acetabular axis, lowering anterior point of iliac blade 18 to 20 degrees below axis of vertebral column, in contrast to 4 degrees in *Diplodocus*, a bifid-spined genus, and 7 degrees in the single-spined genus, *Haplocanthosaurus*; metapophyseal spurs directed lateroventrally on all dorsal and sacral neural spines; prediapophyseal spurs projecting from anterior face of diapophyses on dorsal transverse processes; diagonal bone-struts connecting metapophyseal spurs on second and third sacral neural spines with subhorizontal supracostal plates on dorsal edge of third and fourth sacral ribs. All other North American Jurassic sauropods, including *Apatosaurus*, *Diplodocus*, *Camarasaurus*, and the single-spined *Haplocanthosaurus*, lack such plates, spurs, and bone-struts; chevrons on anterior third of tail one-third longer than those of *Camarasaurus supremus* Cope, as arbitrarily arranged by Osborn and Mook (1921).

DESCRIPTION.—*Cathetosaurus* is assigned to Camarasauridae Cope (1877) on the basis of its general structural affinities to that family, particularly in its axial and appendicular

skeletons, including; bifid cervical and thoracic neural spines; strongly opisthocoelous presacral vertebrae; heavy thoracic ribs; ischium with long, slender shaft not distally expanded as in the Apatosauridae and Diplodocidae; pubis thick and massively constructed, distally flattened but not rounded as in the Apatosauridae, Diplodocidae, and *Haplocanthosaurus*.

At least seven specialized skeletal structures in *C. lewisi*, not seen in any other camarasaurid genus nor in any other sauropod family, qualify the specimen as a new genus and species. These unique features include, but are not restricted to: (1) neural spine bifurcation (Fig. 6B) beginning directly behind the atlas/axis on spine number three, instead of at the fifth or sixth spine, as in almost all other sauropods. Bifurcation continues from the third cervical spine to the last dorsal, or first presacral, spine, in which the apex of the spinal crest is compressed anteroposteriorly and slightly indented but not bifid. The depth of bifurcation is greatest through the cervicodorsal transition, diminishing to the indented crest in the first presacral spine. The cervicodorsal transition was well preserved in the skeleton as found, but badly damaged during collection, obscuring the precise vertebrae involved.

(2) Pre-epipophyseal ridges (Fig. 5a [per]) extending anteriorly from the epipophyses, lateral to the suprapostzygapophyseal laminae, on the superior surface of the cervical postzygapophyses. These ridges pass the base of the neural spine laterally (Fig. 5A) and extend to, or near, the anterior margin of the transverse process and are functionally coequal with prediapophyseal spurs on the dorsal transverse processes, inserting spinal ligaments originating on the metapophyses of the preceding neural spine.

(3) Prediapophyseal spurs (Figs. 3B, 5B₁–B₂) project from the anterior diapophyseal faces of the transverse processes on all dorsal vertebrae (Fig. 9A–B).

(4) Metapophyseal spurs (Figs. 3B–C, 4B₁, 5A–C, 6B, 9A–B) on lateral borders of the spinal metapophyses. Apparently strong ligature originated on these spurs, passing diagonally, posteroventrally, to insert on the prediapophyseal spurs located anteriorly on the diapophyses of the transverse process of the succeeding vertebrae (Fig. 9A).

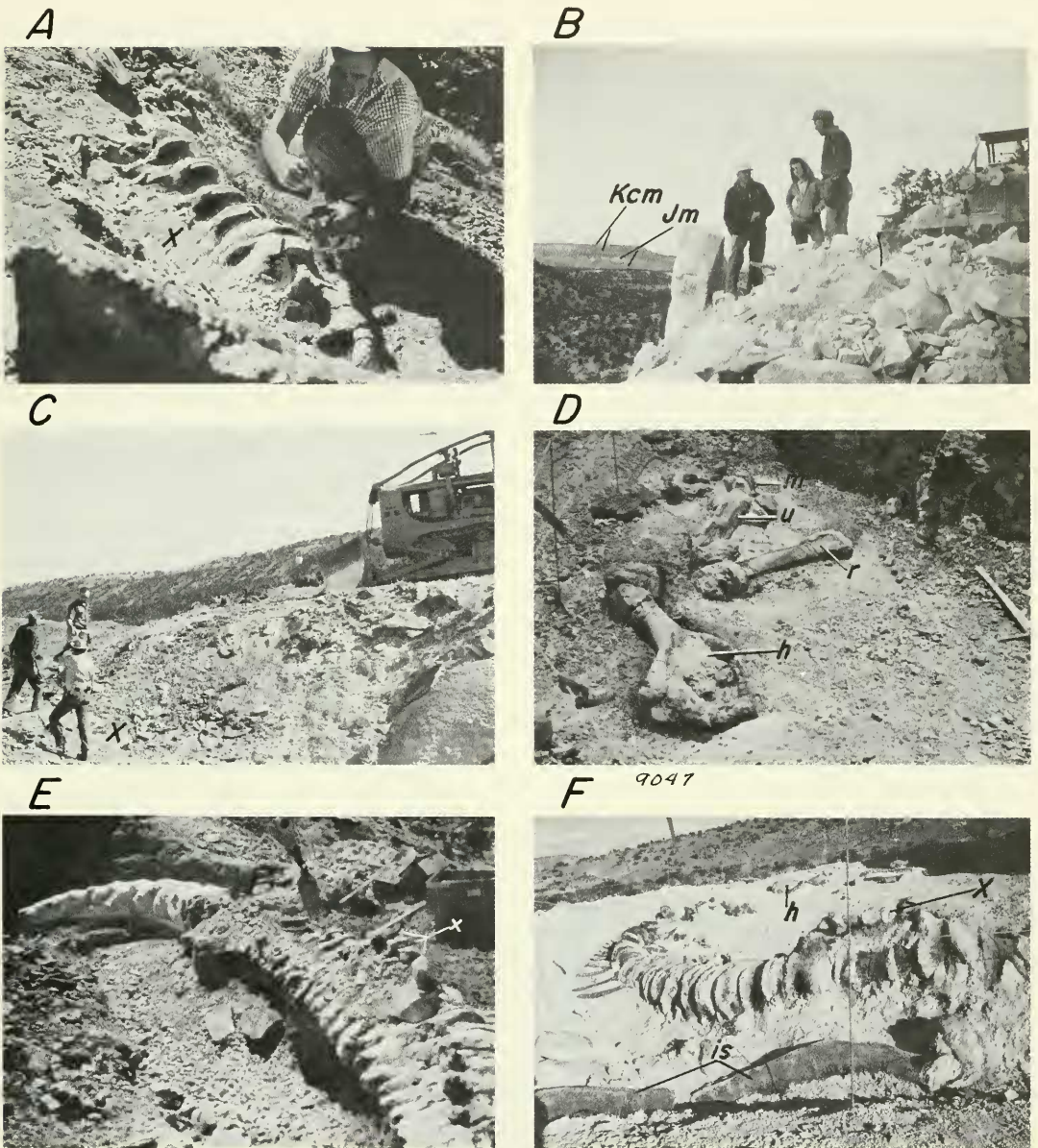


Fig. 1. Discovery and working at Dominguez/Jones Quarry: A, exposed right side of sacral vertebrae at discovery point; B, road building from top of Dakota Sandstone down to Morrison Formation; figures left to right, D. E. and Vivian Jones, discoverers of locality, Mike Heinz, excavator; C, beginning of excavations; D, forelimb and partial manus of *Cathetosaurus lewisi*; E, skeleton of *C. lewisi*; F, ischia and caudal section of *C. lewisi* partially excavated. Abbreviations: h—humerus; is—ischia; Jm—Jurassic Morrison Formation; Kcm—Cretaceous Cedar Mountain Formation; m—manus; r—radius; u—ulna; X—discovery point.

(5) Subcircular supracostal plates, disposed in a near-horizontal plane on the dorsal edge of the sacral ribs (Fig 4C [sp]) with ligature and bone-struts from metapophyseal spurs (Figs. 4B₁, C₁) inserting their anterior borders. These plates originated sacrocaudal

musculature passing caudad to insert serially on caudal neural arches.

(6) Sacral bone-struts connecting metapophyseal spurs with supracostal plates. These struts may have ossified from diagonal ligaments between sacral metapophyseal spurs

and supracostal plates (Fig. 4C₁ [ds, sp]).

(7) Ilii rotated around a transverse acetabular axis, lowering the anterior iliac processes approximately 0–20 degrees, ventrally, below the axis of the vertebral column (see definition of 0 in Fig. 2A), compared to 4 degrees in *Diplodocus* sp. (Fig. 2B), and 7 degrees in *Haplocanthosaurus* sp. (Fig. 2C). Orientation of the ilia to the sacral vertebrae in the composite pelvis of *Camarasaurus*, restored by Osborn and Mook (1921, Fig. 2D) may be incorrect, being modeled with its anterior iliac points located above instead of below the sacral vertebral axis.

DISCUSSION.—Discussed below are some of the most significant structural features identifying *C. lewisi* as novel and the only North American Jurassic sauropod identified to date capable of voluntary bipedalism. *C. lewisi* possessed an interspinal channel carrying the ligamentum nuchae–ligamentum apicum dorsalis complex from skull to pelvis. This channel is formed of bifid neural spines, involving the majority of neural arches between the skull and pelvis. The length of this channel contrasts with much shorter intraspinal channels in all other sauropods, such as *Apatosaurus* (Gilmore 1936), in which bifurcation begins in the fifth to sixth cervical neural arch and ends in the fifth to sixth dorsal neural arch. Being shorter than the interspinal channel in *C. lewisi*, the same channel in bifid-spined sauropods provided a ligamentaceous, long-muscle group of limited length, restricting its effectiveness to elevating the neck, whereas extension of the interspinal channel from skull to pelvis in *C. lewisi* provided an elongate muscle complex capable of elevating the entire preacetabular body from skull to pelvis. This previously undescribed interspinal channel length is here deemed *prima facie* evidence of an ability to assume and sustain a bipedal posture. The continuum of massive soft-tissue flexors filling an intraspinal channel from skull to pelvis demonstrates a complete involvement of the preacetabular body, including the skull, neck, forelimbs, and thorax, as the anterior body rotated around a transverse acetabular axis allowing the genus to attain a balanced, bipedal stance. Supporting this claim, the long chevrons (Fig. 7D), compared with other genera in the Camarasauridae, increased the anterior sagittal plane and, consequently,

weight of the tail, providing a more effective counterbalance to preacetabular weight.

A remarkably strong diagonal intervertebral reinforcement system of ligaments between neural spines and transverse processes in all presacral neural arches is demonstrated in *C. lewisi* by the presence of pre-epipophyseal ridges on cervical neural arches (described below); matching intervertebral, prediaphyseal, and metapophyseal spurs on dorsal neural arches; and by diagonal intervertebral bone-struts or ligaments in the sacrum, the four or five sacral spines being thus diagonally connected to supracostal plates on the dorsal edge of the sacral ribs. The principal function of prediaphyseal spurs is adduced to be the insertion of strong muscles and ligature from metapophyseal spurs on neural spines (Figs. 9A–B) of the preceding vertebra. This method of intervertebral cross-, or diagonal, bracing and reinforcement may have been present to some degree in all sauropods, but the importance of such a system in *C. lewisi* is evident by the prominence of the rugose, spurlike processes at the points of origin and insertion of the diagonal ligaments (Figs. 5B–C). The pre-epipophyseal ridges extending forward from the cervical epiphyses (Fig. 8A [per]) were independent from, and parallel to, the suprapostzygapophyseal laminae (Fig. 8A [spozl]), providing for intervertebral cross-bracing in the cervical series of *C. lewisi*. These epipophyseal ridges originate on the superior surface of the postzygapophyses, bypassing the base of the neural spine to reach the anterior margin of the transverse processes. Epipophyseal ridges and metapophyseal and prediaphyseal spurs (Figs. 3B–B₁) are evidence of a stronger ligamental connection between dorsal neural spines and transverse processes than is claimed or inferred in the analysis of any previously described sauropod. For clarity, interspinal cross-bracing in *C. lewisi* is further described as strong tendons attaching each neural spine to the distal end of the diapophysis on the succeeding transverse process. This diagonal reinforcement was effected by ligaments in cervical and dorsal vertebrae, and with ligaments on three sacral neural arches and bone-struts on two others (Figs. 9A–B). These bone-struts connect the second sacral metapophyses to subhorizontal supracostal plates (Fig. 3C) on the dorsal

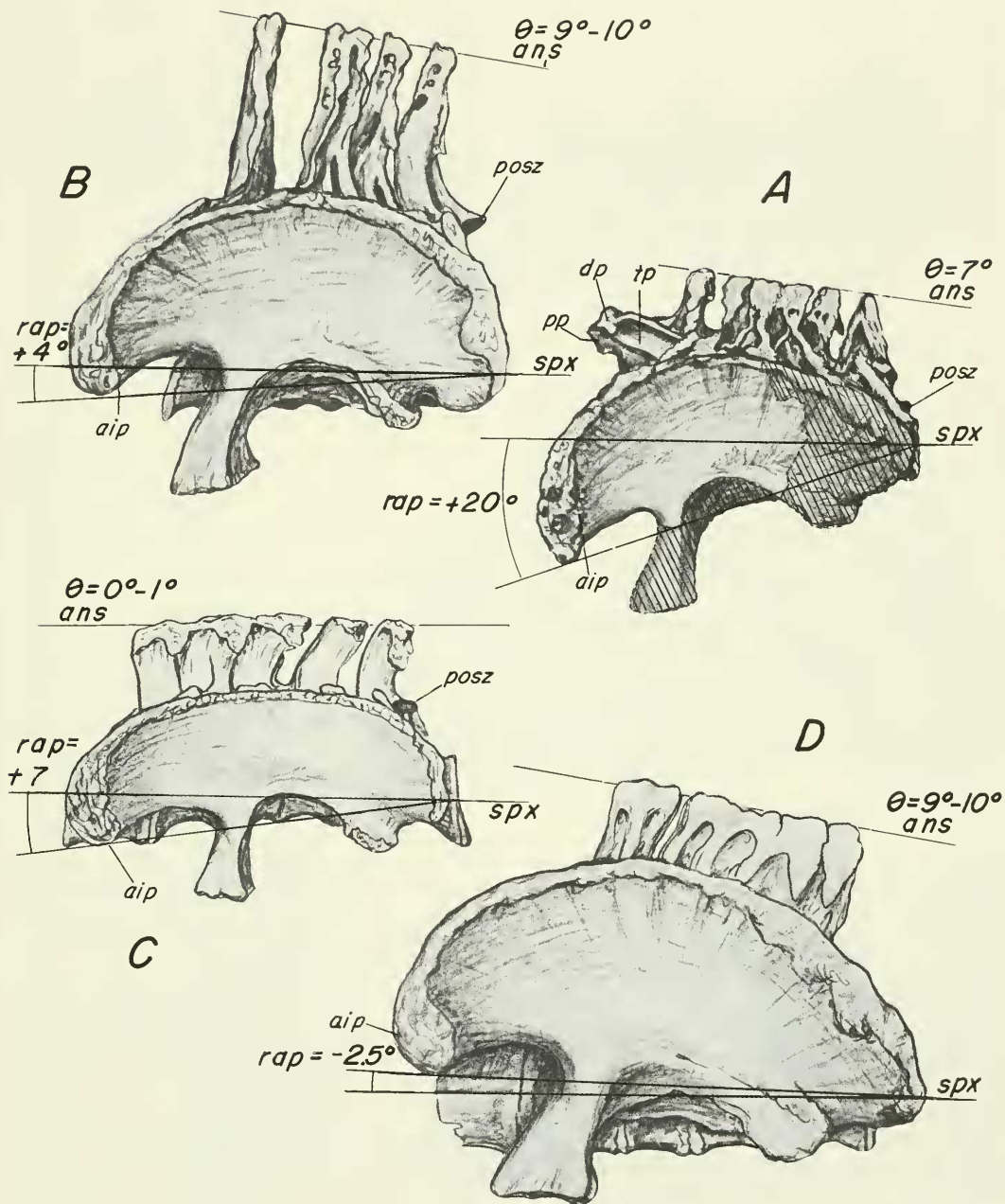


Fig. 2. Four sauropod pelvises: A, *Cathetosaurus lewisi*; B, *Diplodocus carnegii*; C, *Haplocanthosaurus priscus*; D, *Camarasaurus supremus*. Abbreviations: aip—anterior iliac process; θ —angle between vertebral axis (spx) and apices of neural spines (ans); rap—degrees of rotation of anterior iliac process counterclockwise below vertebral axis. Drawings not to scale.

edges of the third sacral ribs; bone-struts connect the third sacral metapophyses to supracostal plates on the dorsal edges of the fourth sacral ribs (Fig. 4C₁). The presence of such a

well-developed system of intervertebral diagonal bracing is seen here as an advantage in elevating the preacetabular body to a bipedal stance by providing highly integrated,

relatively inelastic, connective tissue between skull and pelvis, and once in a bipedal-tripodal position a reinforced vertebral column may have been an advantage in successful bipedal activities. Rudimentary metaphyseal spurs occur on the sacral neural spines of other mature sauropods, including *Diplodocus* (Holland 1901), *Camarasaurus* (Osborn and Mook 1921), and *Haplocanthosaurus* (Hatcher 1903), but in those genera no diagonal bone-struts are present connecting their rudimentary spurs to sacral ribs. These three genera also lack prominent predi-apophyseal and dorsal metaphyseal spurs and independent cervical epipophyseal ridges. Hatcher (1901) notes that in *Diplodocus*

the inferior blades of the diapophyseal laminae are broadly expanded in the anterior caudals and terminate externally and superiorly in broad rugosities, providing great surface for the attachment of the powerful dorsocaudal musculature, which in life may have aided in the alteration of anterior body position from the usual horizontal or quadrupedal position to a more erect bipedal or tripodal position . . . [which] was perhaps less frequently assumed during the life of the individual.

Diplodocus lacked the more basic structural reinforcements and morphological adaptations supporting bipedalism, which are present in the skeleton of *C. lewisi* (this paper).

Subcircular supracostal plates provided an anchoring junction for ligaments and bone-struts extending from the sacral spines to stabilize the supracostal plates against the posterior pull generated by contraction of strong sacrocaudal musculature. These supracostal plates (Figs. 3C, 4C-C₁), with their distal borders depressed 10 to 15 degrees, rest subhorizontally on the dorsal edge of the sacral ribs. The superior surfaces of the plates are striated, with the striae overriding anterior and posterior margins of the plate, parallel to the axis of the vertebral column and to the antero-posterior line of stress generated by powerful sacrocaudal musculature during bipedal activities.

Ventral rotation of the anterior end of the ilium to a comparatively extreme degree around the acetabular axes maintained a center of gravity, or locus of force, within the strongest cross-section of the acetabulum when the anterior body was elevated to a bipedal posture. This 20-degree rotation of

the ilia, relative to the sacral vertebrae, in *C. lewisi* (Fig. 2A), verified by co-ossification of all pelvic elements, is interpreted here as strong evidence for persistent, voluntary bipedalism. When the anterior body was elevated to a bipedal stance, the most heavily buttressed sections of the acetabulae were rotated to an optimum weight-bearing position above the femoral axes, whereas in other sauropods, except the brachiosaurs (discussed later), elevation of the anterior body with the concomitant rotation of the pelvis around a transverse acetabular axis would have positioned a major portion of body weight on the weakest midshaft, unbuttressed cross-section of the pubic peduncle. An additional advantage achieved by the 20-degree ventral rotation of the anterior iliac processes in *C. lewisi* may have been that of increased support to the ventral surface of the visceral mass during bipedal posture. This support could have been provided in a manner similar to, but to a lesser degree than, that seen in the large edentates such as *Megatherium americanum* Cuvier and *Megalonyx jeffersoni*, which were habitual bipedal arboreal feeders (Scott 1937). The anterior iliac processes of these edentates flare out on a subhorizontal plane, adding support to their visceral mass during bipedal activity. Compared with *C. lewisi*, the position of the anterior iliac processes in most other sauropods could have offered little support to the ventral surface of the visceral mass, were those sauropods capable of raising their anterior body to an erect, bipedal stance.

Orientation of the ilia to the axis of the sacral vertebrae in apparently obligate quadrupeds, such as the Diplodocidae and Titanosauridae, when verified by co-ossification of all pelvic elements, was generally less than 10 degrees (Fig. 2). However, the brachiosaurs with single neural spines throughout their spinal column—and for which, as far as I am able to learn, no well-preserved pelvis exists to be measured—may have evolved anteroventrally rotated ilia similar to the ilio-sacral relationship seen in *C. lewisi*.

The thorax in the Brachiosauridae was significantly elevated by front limbs equal to, or longer than, rear (Riggs 1921, Janensch 1936). Because of their great size (80 tons calculated, Colbert 1983), members of this family were probably obligate quadrupeds. Elevation of their thorax on long front limbs would have

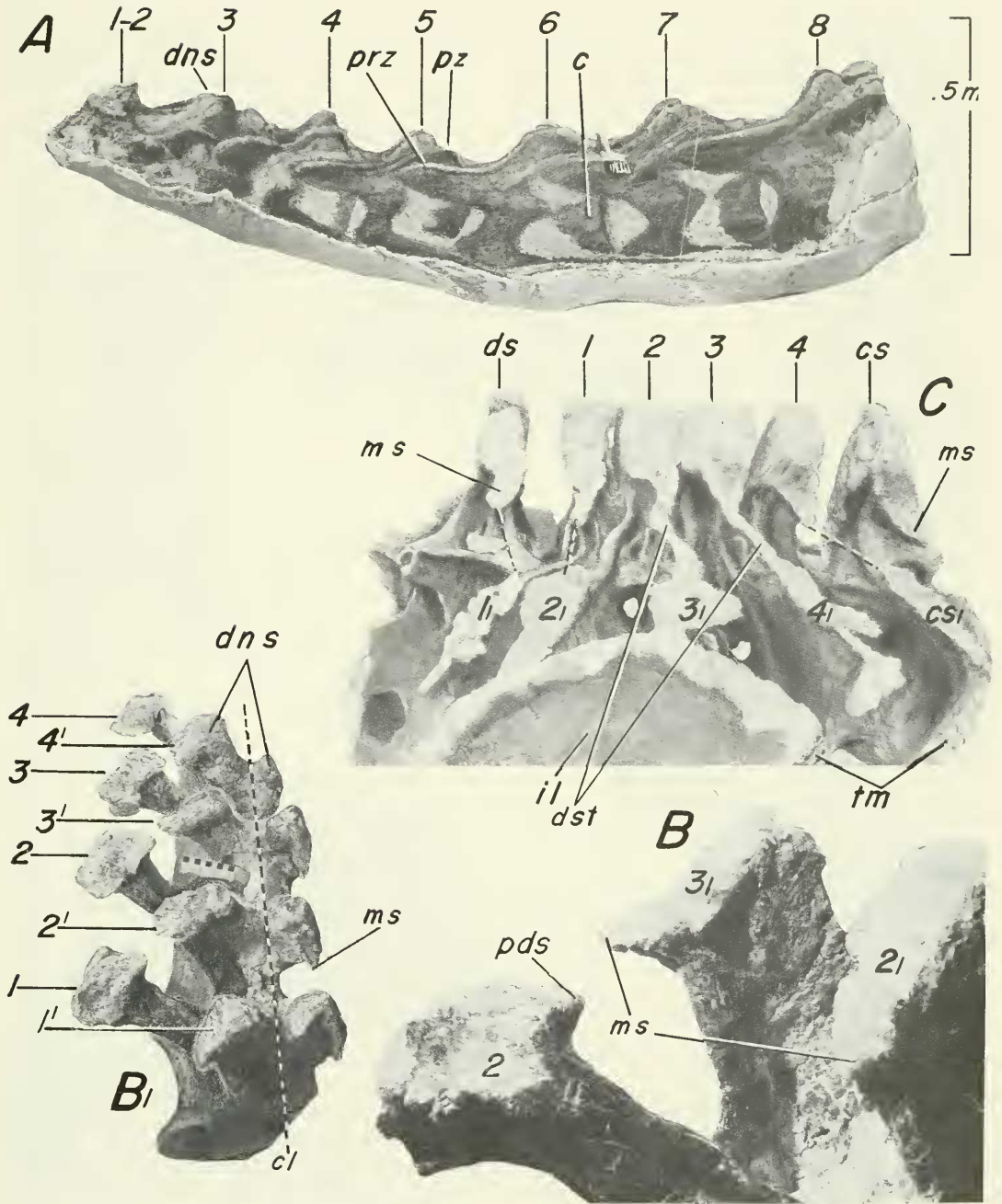


Fig. 3. Cervical, sacral, and dorsal vertebrae of *Cathetosaurus lewisi*: A, 1-8, cervical series from atlas/axis to number eight (partially prepared). B-B₁, metapophyseal (lts) and prediapophyseal (pds) spurs on *C. lewisi* presacral vertebrae. B, two metapophyseal spurs (lts), one prediapophyseal spur (pds). B₁, four transverse processes (1-4), four metapophyses (1_l-4_l): 1, 1_l are on same neural arch, posterodorsal view. C, *C. lewisi* sacrum with supracostal plates (1_l-csl), neural spines (ds-cs), left lateral view. Abbreviations: c-centrum; cl-center line; cs-caudosacral; csl-caudosacral supracostal plate; dns-bifid neural spines; ds-dorsosacral spine; dst-diagonal metapophyseal bone struts to supracostal plates (3_l, 4_l); il-ilium; prz-prezygapophysis; lts-metapophyseal spurs; pds-prediapophyseal spur; pz-postzygapophysis; tm-teeth marks.

rotated their ilia around a transverse acetabular axis, locating the weakest, unbuttressed cross-section of the pubic peduncular shaft above the femoral axis—if the anterior ilium was in fact ventrally rotated less than 10 degrees below the spinal axis, as it is in other sauropod families including the Apatosauridae and Diplodocidae. I collected a *Brachiosaurus* ilium (described elsewhere) from the Uncompahgre fauna in 1975 and verify the shaft of the pubic peduncle as being thin and fragile, suggesting the anterior ilium was rotated ventrally, below the spinal axis, in a manner similar to the 20-degree ventral rotation of the anterior iliac processes of *C. lewisi* (Fig. 2A). The only complete brachiosaur pelvis I am aware of is mounted as part of a restored display skeleton standing in the Museum für Naturkunde, Berlin (Janensch 1936). In this mount the anterior iliac processes appear to be ventrally rotated approximately 15 degrees below the spinal axis; however, I have been unable to find a report on the accuracy of the restoration.

The pubic and ischiadic peduncles of *C. lewisi* are missing from the only ilium present with the skeleton (Figs. 4C–C₁), and so their relative strength and morphology are incompletely known except that, as previously noted, the 20-degree ventral rotation of the anterior end of the ilium, relative to the spinal axis, is verified by co-ossification of all pelvic elements present (Fig. 2A).

Jurassic sauropods such as *Barosaurus*, *Diplodocus*, and *Apatosaurus*, none of which had anterior iliac processes ventrally rotated more than a few degrees below the spinal axis, nor which displayed significant evidence of structural reinforcement of the spine and pelvis, were recently illustrated (Bakker 1986) as habitual, bipedal, arboreal feeders, although no convincing structural evidence to support such a claim is provided, except to note the possible value of tall sacral spines. The incompletely known sauropod *Barosaurus* was also illustrated by Bakker (1986) in an erect, bipedal pose, foraging high in trees, despite a considerable lack of important information on its skeleton. Lull (1919) illustrates *Barosaurus*, known from only one partial, badly eroded skeleton. This material consists of 4 incomplete posterior cervical vertebrae, 10 dorsal and 19 caudal vertebrae, a massive chunk of sacrum, and fragments of a badly

eroded appendicular skeleton. Lull's restoration (1919: Pl. VII), overlaid on a partial skeleton of *Diplodocus* for comparison, interprets the basal cervical and anterior dorsal vertebrae of *Barosaurus* as indicating a distinct upward flexure at the base of the neck, a feature not reported in other Jurassic sauropods. This upturn flexure at the base of an apparently long neck would have allowed *Barosaurus* to feed arboreally as a quadruped, providing a convincing alternative to Bakker's (1986) representation. Marsh (1890) placed *Barosaurus* in the Atlantosauridae, together with *Atlantosaurus* and *Apatosaurus*, while describing it as "being very much like *Diplodocus*."

In addition to Bakker (1986), other authors (McLoughlin 1979), ignoring the empirical demands of biomechanics, have painted fanciful scenarios depicting various sauropods as being capable of voluntary bipedalism. McLoughlin (1979:60) even suggests a prehensile tail on *Diplodocus*, wrapped around a tree "to steady itself on its hind legs." None of these imaginative claims is supported by verifiable evidence from structural morphology published in legitimate scientific descriptions. The present paper is the first to definitively describe a sauropod capable of sustained, voluntary bipedalism, with incontrovertible evidence recovered from existing skeletal elements.

The hypothetical postural transition from a bipedal prosauropod to a heavy quadrupedal sauropod (Romer 1956) may have occurred as an evolutionary response to environmental and other factors; but, prior to this paper, the notion that after becoming heavily quadrupedal, optional bipedalism was still possible, was without any substantiating physical evidence. Some sauropods may have been able to rise up momentarily to a semibipedal, or tripod posture, but none, prior to the discovery of *C. lewisi*, display any convincing structural, or morphological, evidence of a capability for a sustained, bipedal posture.

Various relevant factors apply to this paper's claim that bipedalism in sauropods is presently restricted to one species, and these factors need further discussion.

SAUROPOD BIPEDALISM

The relevant laws of physics cannot be ignored in calculating the probable stresses

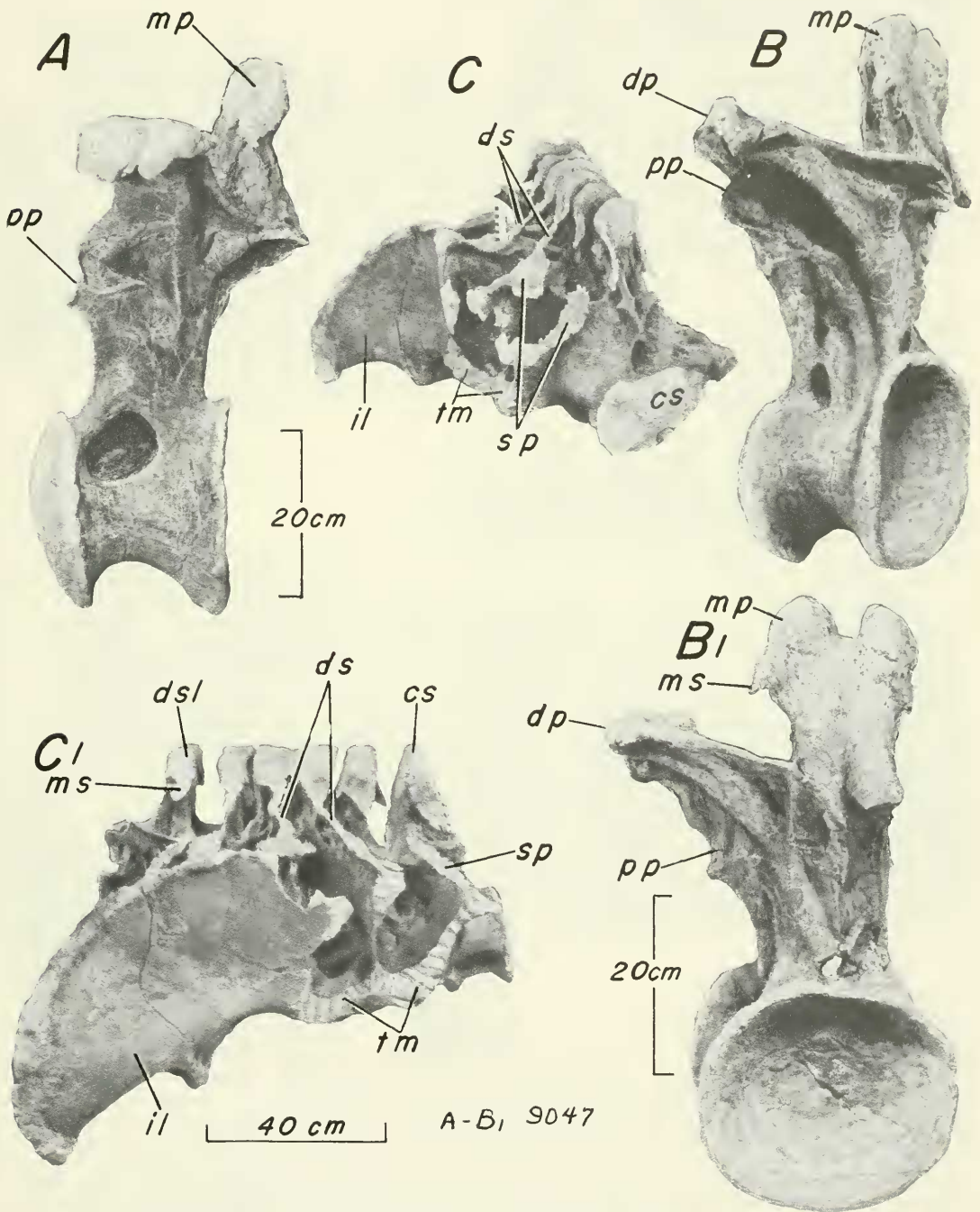


Fig. 4. *Cathetosaurus lewisi* presacral vertebrae and sacrum: A, second presacral vertebra, left lateral view; B, second presacral vertebra, posterolateral view; B₁, second presacral vertebra, posterior view; C, sacrum, oblique posterior view; C₁, sacrum, left lateral view. Abbreviations: cs—caudosacral vertebra; dp—diapophysis; dsl—dorsosacral vertebra; ds—diagonal bone strut; il—ilium; ms—metapophyseal spur; mp—metapophysis; pp—parapophysis; sp—supracostal plate; tm—teeth marks.

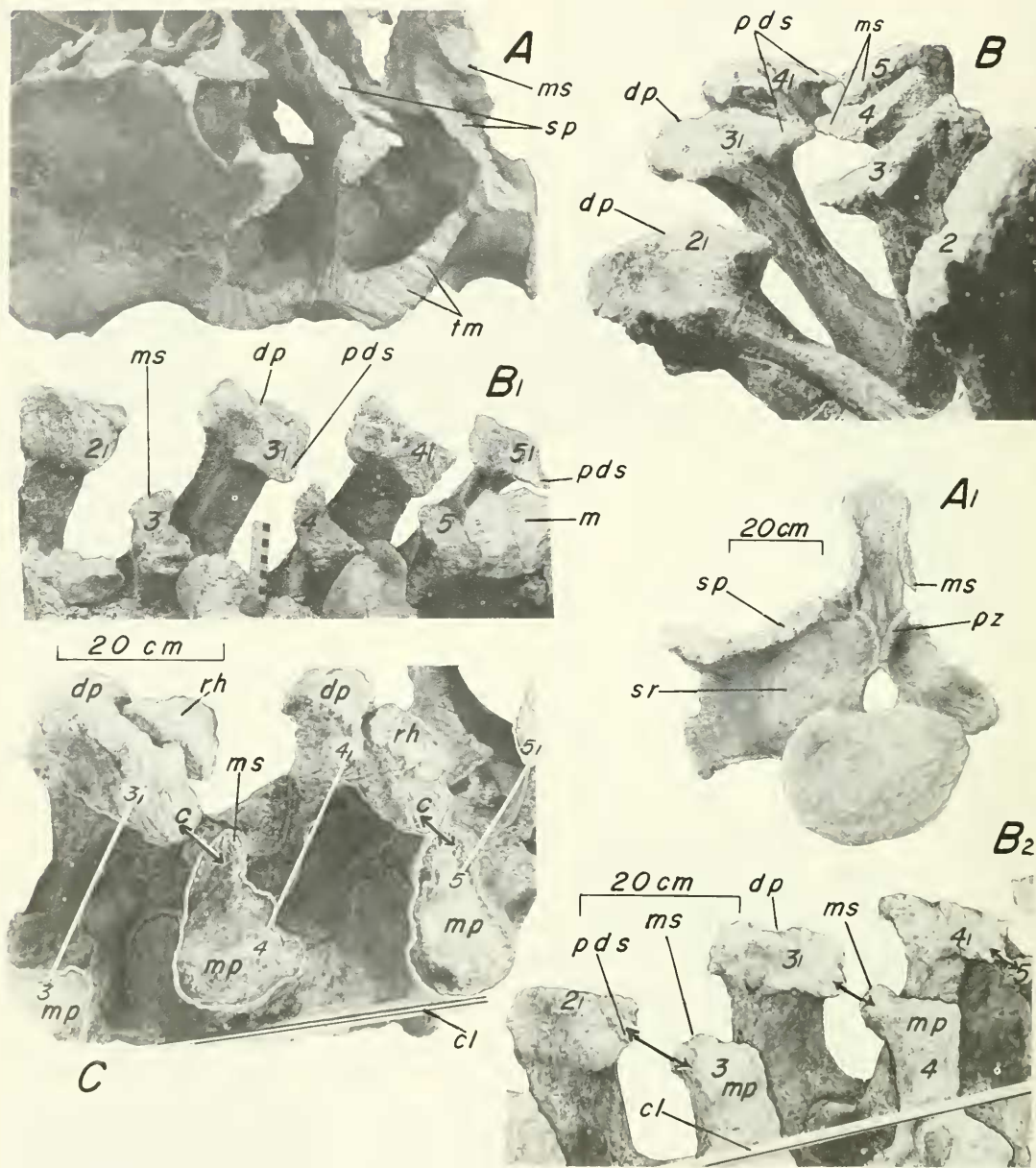


Fig. 5. *Cathetosaurus lewisi* sacrum and details of presacral spines and transverse processes: A, left lateral view of sacrum with teeth marks (tm); A₁, posterior view of sacrocaudal vertebra; B, posterolateral view of presacral metapophyses (2-5) and transverse processes (2_l-4_l); B₁, prediadiapophyseal spurs (pds) and metadiapophyseal spurs (ms); B₂, dorsomedial view of left diapophyses (dp, 2_l, 3_l, 4_l) and metapophyses (3-5) (arrows indicate ligamental connection between prediadiapophyseal spurs [pds] and metapophyses [mp]); C, detail of diapophyses and metapophyses (white lines indicate same neural arch; black arrows [c] indicate ligamental connection between adjacent neural arches by spurs). Abbreviations: cl—center line; dp—diapophysis; lts—metapophyseal spur; m—matrix; mp—metapophyseal spur; pds—prediadiapophyseal spur; pz—postzygapophysis; sp—supracostal plate; rh—rib head; sr—sacral rib.

developing in a large sauropod's skeleton if, as an obligate quadruped, it made an attempt to rise to a bipedal posture and its many tons of

weight, calculated from 80 to 100 tons (Colbert 1983, Halsted and Halsted 1981), were transferred from four legs to two. Not only

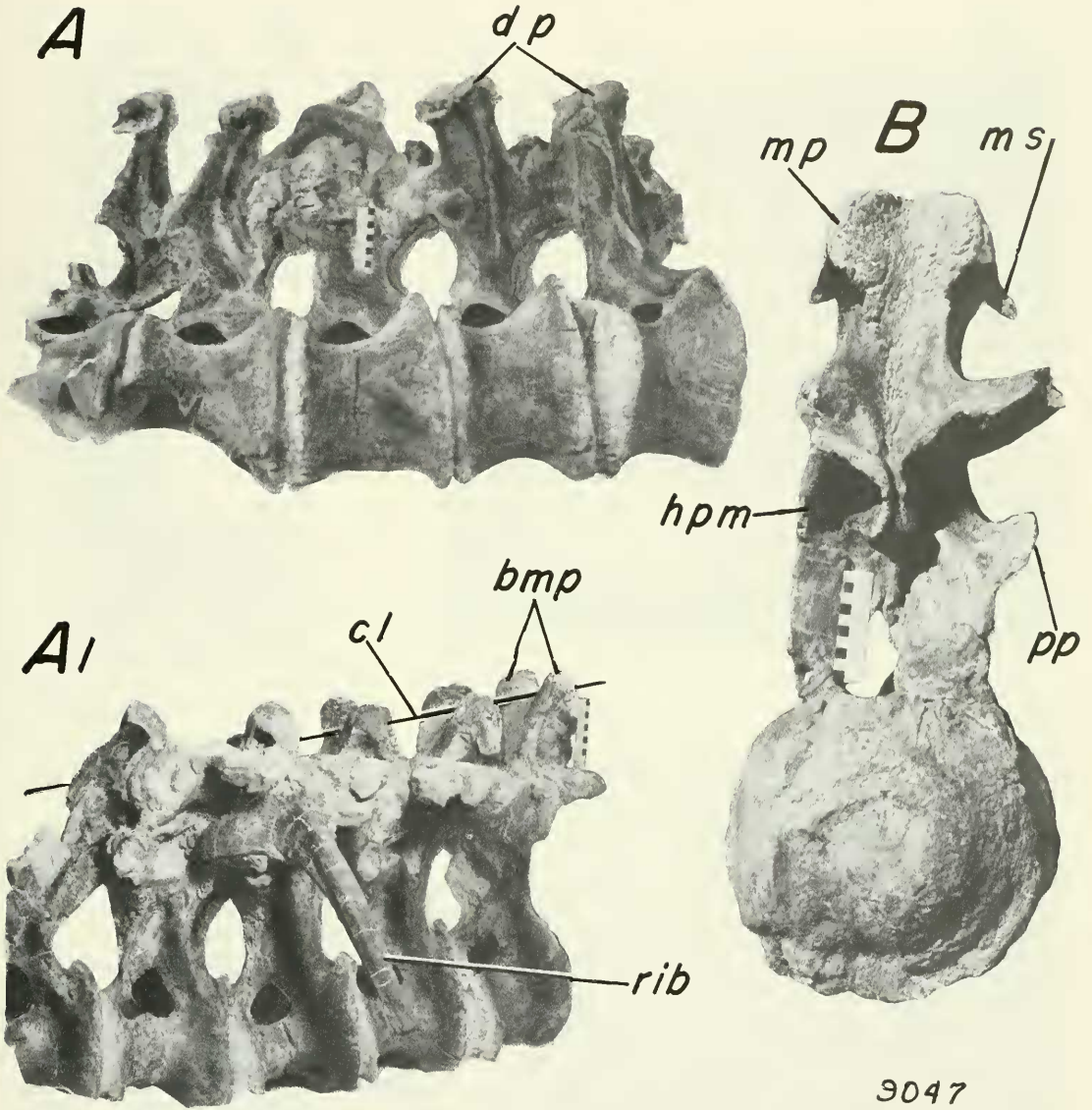


Fig. 6. Six *Cathetosaurus lewisi* presacral vertebrae: A, ventral view (centrum width equal to length); A₁, lateral view (centrum length greater than height); B, dorsosacral, or first presacral, vertebra, anterior view. Abbreviations: bmp—bifid metapophyses; cl—center line; dp—diapophyses; hpm—hypantrum (closed by crushing); mp—metapophyseal spur; ms—metapophyseal spur; pp—parapophysis.

would its skeletal structure be inadequate for such a massive weight shift, but its musculature would lack the necessary adaptation and strength to support the surge of such an overload.

Physical laws pertaining to the design and operation of heavy, modern, self-propelled machines, such as cranes and caterpillar trac-

tors, would no doubt have applied equally to the behavior of 80-ton animals in the Mesozoic Era. One modern bipedal, earth-moving machine with a weight comparable to that of a medium-sized sauropod is the D-8 Caterpillar tractor. With a blade it weighs approximately 34 tons, or considerably less than half the 80 tons estimated for a large sauropod

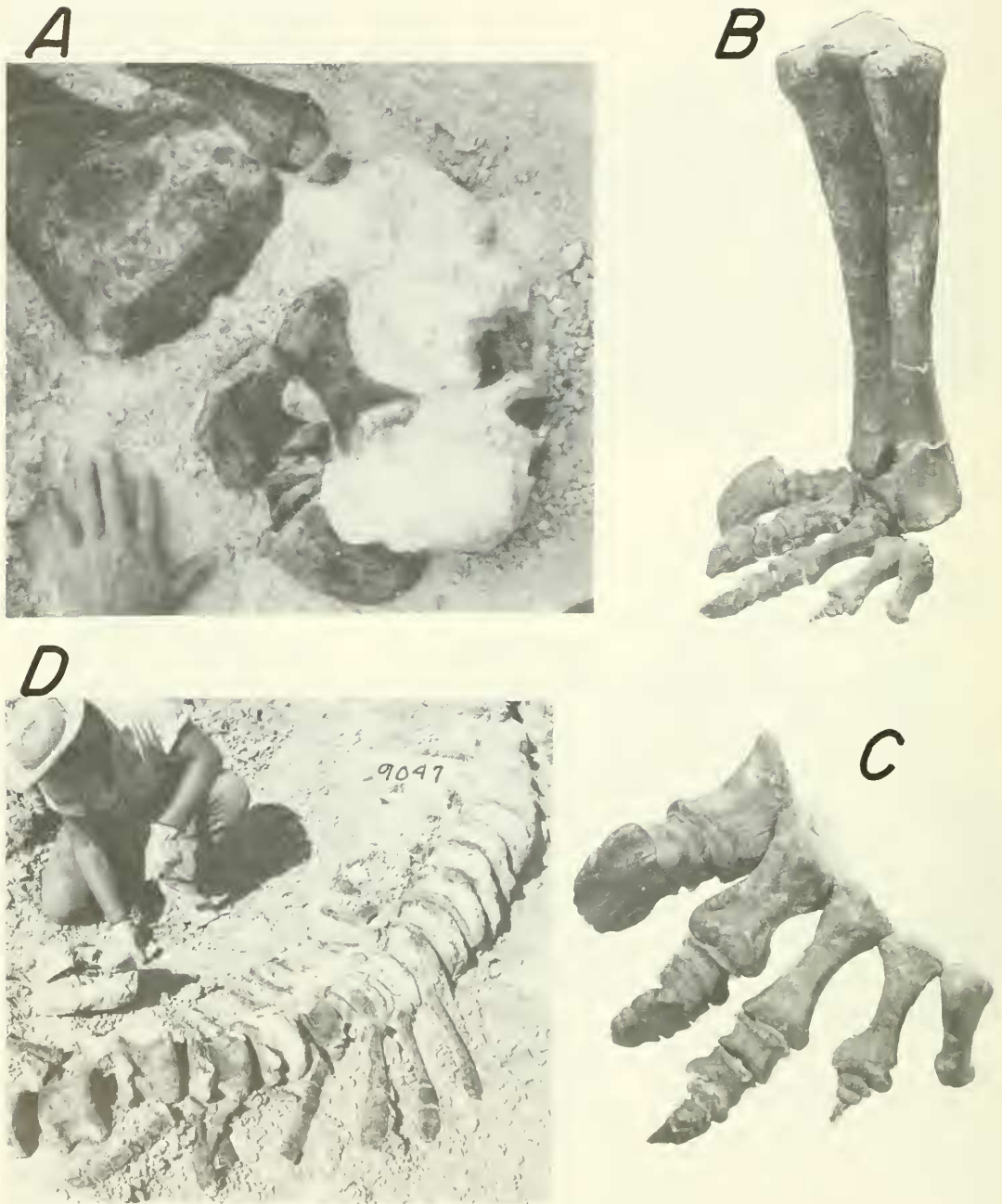


Fig. 7. A, *Camarasaurus* sp. left rear foot in concretion; B, same as A, prepared; C, detail of pes with four unguals; D, anterior section of *C. lewisi* caudal vertebrae with first seven chevrons (much longer than neural spines).

(Colbert 1983:45). Bipedal supports distribute the tractor's weight over an area of more than 50 square feet by means of two endless jointed tracks, while the weight of a large sauropod, standing on its rear legs,

would have been supported on a total footpad area of approximately 12 square feet, if that footpad area is generously calculated as six square feet for each rear foot, based on Gilmore's (1936) calculations of 27×31 inches

as the approximate size of the *Apatosaurus louisae* pes. This is approximately one-fourth the area supporting the much smaller 34-ton tractor.

A vertebrate skeleton is like a machine: a structural arrangement of rigid parts and the functional range of motion in both systems is governed by the mechanical design of those rigid parts. The capability for motion and acceleration in both systems is strongly affected by interacting factors: inertia and balance; the influence of gravity over mass during motion and acceleration; mechanical sophistication in the weight-support and locomotion systems, and the requirement of a suitable substrate on which to function; an energy supply, and the unit's efficiency in transforming that energy into motion. Most of these factors would affect a sauropod's mobility and speed, but the primary concern here is simply the matter of the structural and muscular adaptations necessary to elevate and support a large quadruped, particularly a sauropod dinosaur, in an upright posture with its rear legs and tail in tripod contact with the ground.

In raising a heavy beam to a vertical position the greatest structural stress and the maximum energy demand are imposed by gravity at the beginning of elevation, when the mass is horizontal and furthest from a vertical line above the fulcrum, and the angle between the rising structure and the horizon is smallest, such as the angle of applied stress occurring when a construction crane begins elevating a long boom from the ground.

Physical laws affecting the successful elevation and operation of modern crane booms no doubt applied as well to a sauropod attempting to elevate its anterior body and function bipedally. The acetabulum is the basic pivotal point in all bipedal and quadrupedal vertebrates. Thus, in any sauropod adapted to bipedalism, pelvic design surrounding that pivot could be expected to display some recognizable structural specializations, such as bony reinforcements and processes, to accommodate the additional weight shift from front legs to rear. *Cathetosaurus lewisi* displays bony strengthening and novel processes (Fig. 3C) to a degree significantly greater than that seen in any other described North American Jurassic sauropod.

The prime force elevating the anterior body of *C. lewisi* was generated by several long-

muscle groups combined in an extended series with the M. ligamentum nuchae–M. ligamenta apicum dorsalis complex, supported in an interspinal channel of bifid neural spines (Figs. 6A₁, 9B) from skull to pelvis. These muscles, anterior to the acetabular fulcrum, were counterbalanced and augmented by caudal long-muscle groups originating in the sacrum and inserting serially on caudal vertebrae. The contraction of these presacral and postsacral muscle groups involved most of the spinal column in shifting body weight back toward the rear limbs and tail as the neck and thorax were elevated toward a vertical line above the fulcrum. Tail weight, acting as a counterbalance, aided the shift. Very long chevrons (Fig. 7D), nearly twice the length of those in *Camarasaurus* (Osborn and Mook 1921), increased the area in the sagittal plane of the tail, with a concomitant increase in weight, providing greater postsacral muscularity and improving the strength of the tail for use in bipedal activities.

An equitable distribution of weight in a 50-ton sauropod standing with tail raised, as depicted in various modern illustrations (McLoughlin 1979, Bakker 1986), would have placed a load of 25,000 lbs on the joints of each limb and foot. If the thorax were elevated to a bipedal position, lowering the tail and shifting body weight caudally, 100,000 lbs would be imposed on the pelvis, minus a generous 10 tons for postacetabular weight to be supported by the tail. The remainder would be transmitted through the acetabular area to the rear legs, requiring each rear ankle to support a static load of probably more than 20 tons. Each time the sauropod shifted body position, a temporary surge of increased pressure, and resultant stress, would be imposed on the limb and foot nearest the center of gravity.

A degree of structural sophistication similar to that seen in the feet of proboscidiens was present (Figs. 12A–B) in the extinct, graviportal, long-limbed digitigrade feet of the titanotheres (Osborn 1929). In both, the manual pisiform, and radial processes on other carpal bones, provided muscular leverage to the front foot, whereas no pisiform or other comparable bones were present in the sauropod locomotor apparatus. Sauropods also lacked the pedal calcaneum, which in mammals (Figs. 12B–C₁) is an important lever providing increased mechanical advantage to the

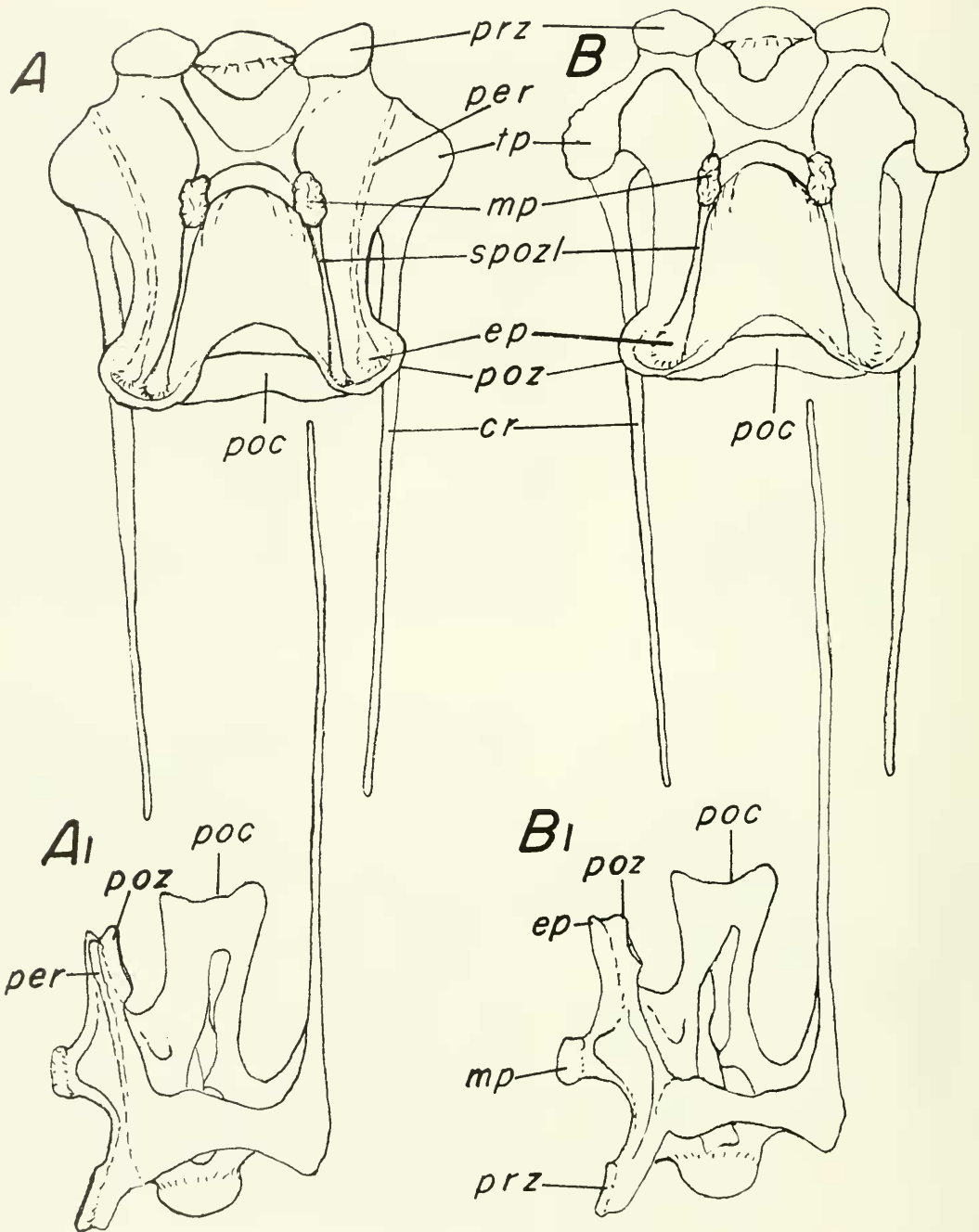


Fig. 8. Line drawing of two sauropod cervical vertebrae with very long cervical ribs: A, A₁, *Cathetosaurus lewisi*; B, B₁, *Uintasaurus (Camarasaurus) douglassi*. Abbreviations: cr—cervical rib; ep—epipophyses; mp—metapophyses; per—pre-cipipophyseal ridge; poc—posterior concavity; poz—postzygapophyses; prz—prezygapophyses; spozl—suprapostzygapophyseal laminae; tp—transverse process.

various muscles, including the M. gastrocnemius—M. plantaris—M. soleus complex, extending the pes.

Pedal extensors in sauropods (if there were muscles large enough to be identified as such) functioned without a calcaneum and

consequently with very little leverage to extend the pes, basically because the area of insertion on the proximoventral borders of the metatarsals was too near the fulcral area on the ventral surface of the astragalus (Figs. 7B, 13A). It cannot be demonstrated, therefore, that sauropods had any significant muscle-leverage system for extending or otherwise manipulating the pes. It probably served in locomotion with little more flexure than the rubber extension on the distal end of a crutch.

The lower front limb extensor in the large mammal *Palaeosyops* (Osborn 1929), the *M. caput laterale* (Fig. 13C [c. la]), enjoys a favorable ratio of leverage to ulnar length of approximately 1 to 2.5, with the olecranon process rising approximately 40 degrees above the center of the humeral joint radius (Fig. 13 [cjr]). The *M. caput laterale* inserts the olecranon process and rocks the ulna across a fulcral surface on the distal end of the humerus to extend the lower limb. No olecranon process is present on the sauropod ulna (Figs. 13A–B) to provide equivalent, advantageous leverage.

I mounted a large, free-standing mammoth skeleton from the LaBrea Tar Pits in the Page Museum in Los Angeles, California (1977), for the opportunity to study and compare limb and foot joint structure in a heavy mammal with the design and function of similar joints in sauropods. The study confirmed that limb and foot joints in the most agile dinosaur, large or small, are structurally and functionally inferior to those of probosidians and, in large measure, to all mammals.

When the elephant does a single, front-limb "handstand" (Asian elephant, Circus of the Stars, CBS-TV, December 1986), the weight of its entire body is transferred to one foreleg. The joints in its scapula, elbow, and wrist withstand the abnormally high pressure in this radical posture because of compact, bone-to-bone joint geometry that includes ball-and-socket joints and curvilinear flanged joints mating perfectly with matching incurvate forms (Figs. 10B–B₄, 11B–E₁) in an articulated system of solid bone, glazed with a thin layer of dense cartilage and encapsulated with lubricating fluid. No equivalent bone-to-bone joint structure is present in sauropods.

FOOT STRUCTURE.—Sauropod feet were of simple construction (Fig. 12E) in contrast to the number of bones and geometric complex-

ity of those in heavy mammals such as titanotheres (Figs. 12A–B). A significant feature of titanotheres limb and foot construction is the very close articulation and almost complete communication of apposing surfaces in the multifaceted bones of the carpus and tarsus (Figs. 12A–B). Another important feature is bones with processes, radial to limb axes, functioning as levers, such as in the pisiform, cuboid, calcaneum, and the ulnar olecranon process. Sauropod limb and foot bones have no equivalent comparable "levers," or compact joint structure, and, therefore, have less comparative potential for strength and agility. This leaves them mechanically inferior to mammals—empirical evidence that various present-day speculators (Bakker 1986, McLoughlin 1979) on sauropod locomotion and physical behavior ignore.

Sauropod foot bones are reduced and simply arranged (Figs. 7C, 12E), lacking the structural sophistication of "lever" bones and large areas of articulating communication present in the compact mass of subrectangular bones in the mammalian carpus and tarsus, in which the bones are conformably shaped and lubricated to move together, pushing as they do so against each other, as the entire group responds to a flow of energy originating in limb muscles during locomotion. By contrast, the number of bones in the sauropod carpus and tarsus was extremely reduced (Fig. 12E), being reported as one bone in the carpus of *Apatosaurus louisae* Holland (Gilmore 1936), which Hatcher (1902) described as the scapho-lunar, and one bone in the tarsus of *Diplodocus* and *Apatosaurus*, reported as the astragalus (Gilmore 1936). Sauropod carpi and tarsi are very poorly known because of the small number of sauropod feet described. However, mobile wrists and ankles were obviously of small importance in sauropod locomotion; otherwise they would have been more sophisticated. In any three-dimensional arrangement of mechanical joints, complex-motion capability decreases in direct proportion to a decrease in the number of participating elements. The result was that sauropod feet had very little circular mobility in their distal spheres on the lower limbs: simply put, sauropods had little wrist and ankle movement.

My study of the LaBrea Tar Pit mammoth revealed that rotary motion of the pes can

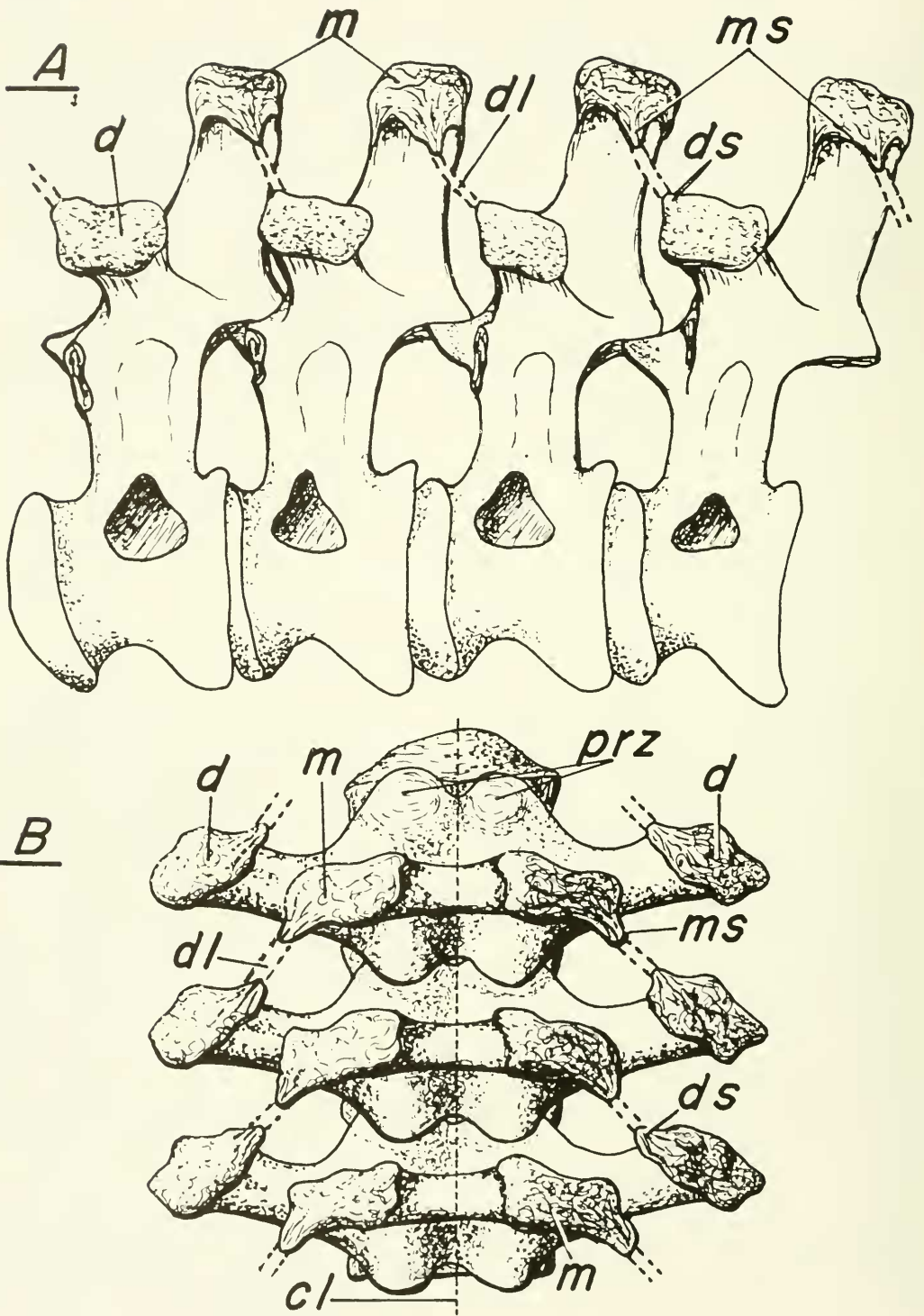


Fig. 9. A, lateral and B, superior views. Scheme of diagonal ligament (dl) bracing in dorsal vertebrae of *Cathetosaurus lewisi*: diagonal ligaments from metapophyses (m) to diapophyses (d) connect all adjacent vertebrae throughout the series. Abbreviations: cl—center line, d—diapophysis, dl—diagonal ligament, ds—diapophyseal spur, m—metapophyses, ms—metapophyseal spurs; prz—prezygapophyses.

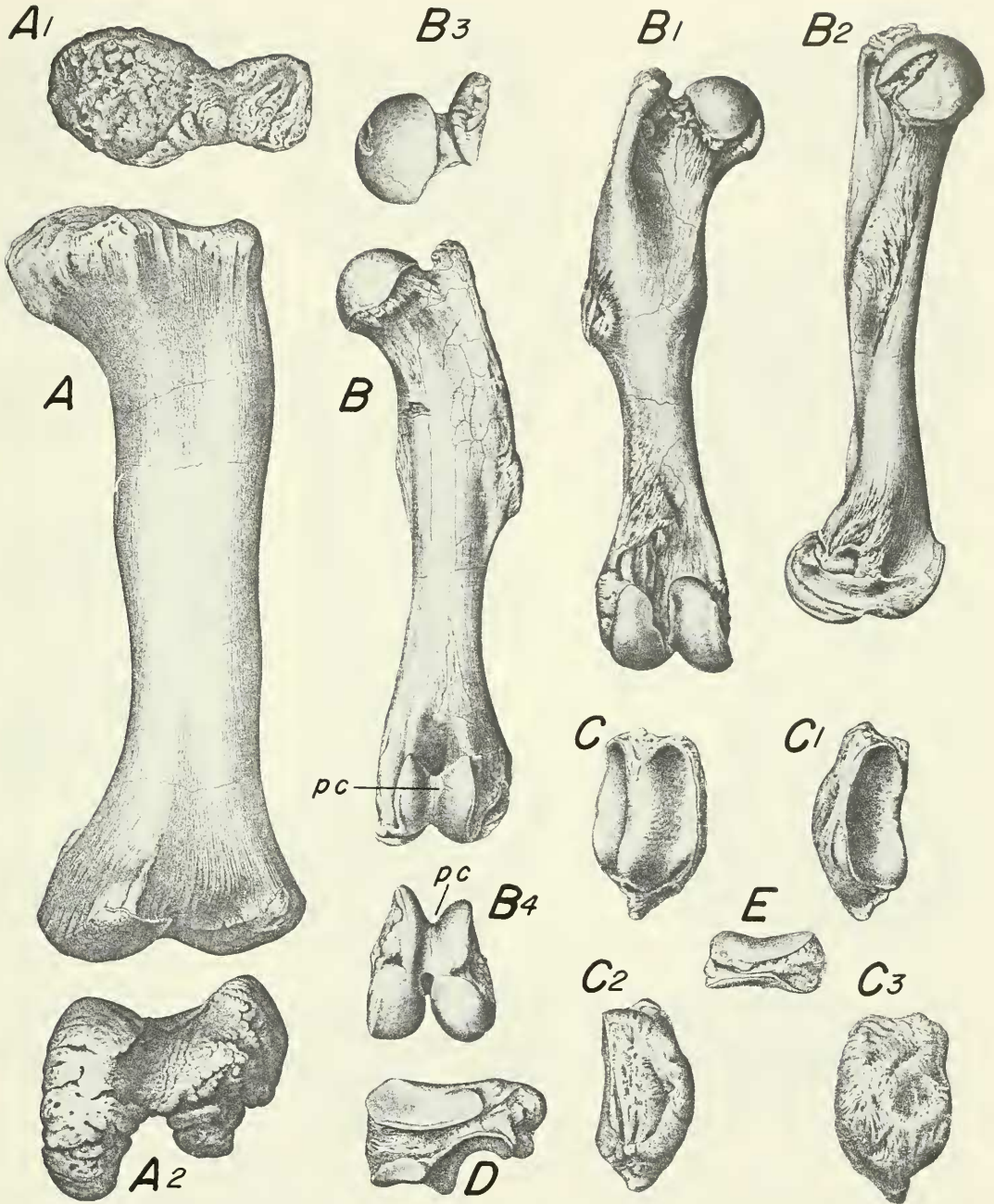


Fig. 10. A-A₁, sauropod dinosaur, Camarasauridae; B-E, mammal, Brontotheridae. *Camarasaurus*: A, left femur, anterior view; A₁, proximal view; A₂, distal view. *Brontops*: A, left femur, anterior view; B₁, posterior view; B₂, medial view; B₃, proximal view; B₄, distal view; C, left patella, posterior view; C₁, lateral view; C₂, medial view; C₃, anterior view; D, left scaphoid, ulnar view; E, trapezoid, medial view. Abbreviations: pc—patellar channel. Not to scale.

occur as a blend of simultaneous movement in separate carpal joint planes, similar to the arrangement seen in titanotheres (Fig. 12A). In this system the manus can swing in a

mediolateral arc on the proximal joint plane at the articulation of the radius-ulna and scaphoid-lunar-cuneiform and then through a second arc, at a right angle to the first,

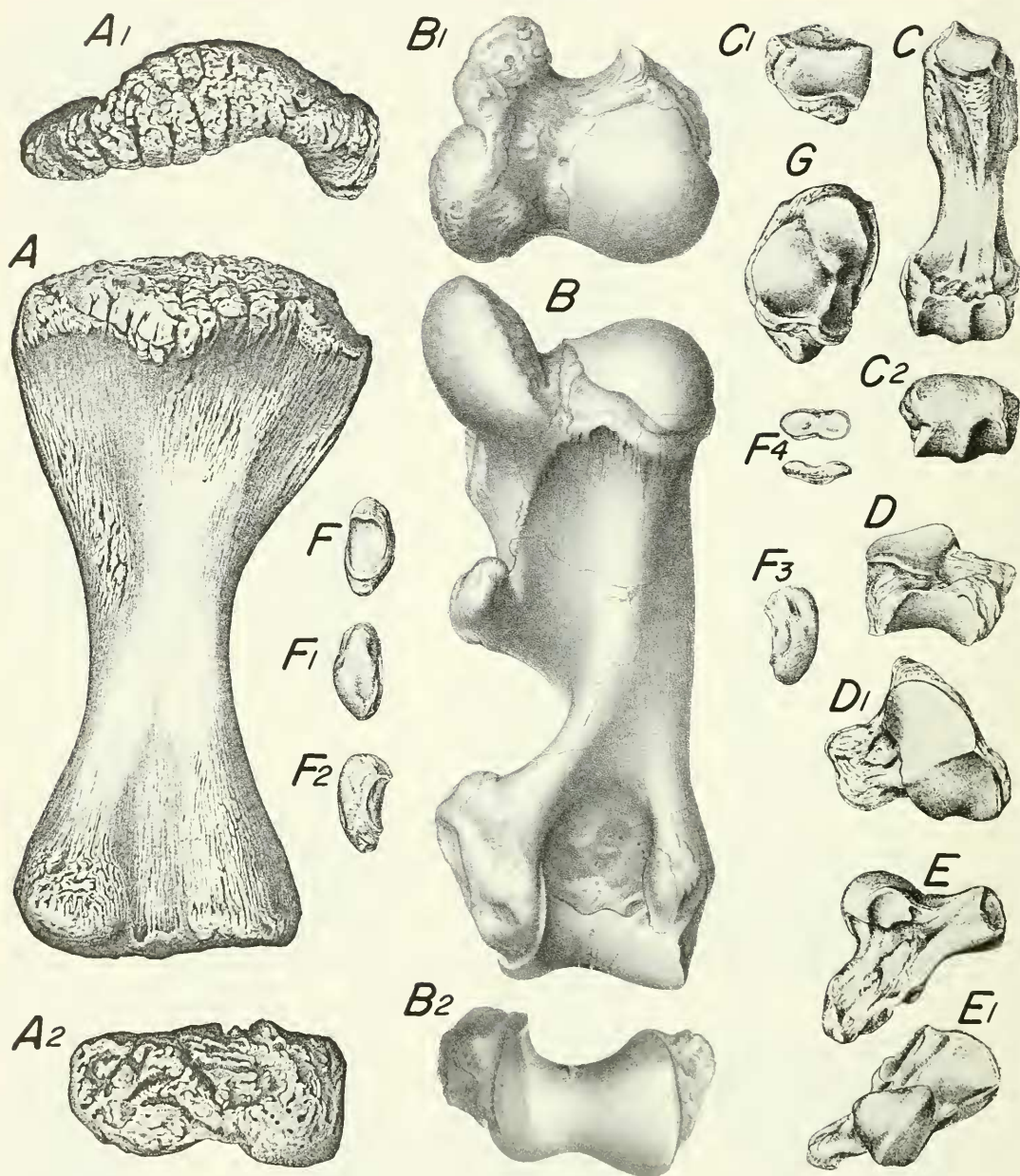


Fig. 11. Sauropod dinosaur, Camarasauridae, A-A₂; mammal, Brontotheridae, B-B₂. *Camarasaurus*: A, left humerus, anterior view; A₁, proximal view; A₂, distal view. *Brontops*: A, left humerus; B₁, proximal view; B₂, distal view; C, fifth, left metacarpal, posterior view; C₁, proximal view; C₂, distal view; D, left, unciform, lateral view; D₁, proximal view; E, left magnum, medial view; E₁, proximal view; F-F₄, left manual sesamoids; G, left scaphoid, distal view. Not to scale.

through the joint plane of the scaphoid-lumarcuneiform and trapezoid-magnum-unciform/pisiform articulation. Rotary motion of the manus does not depend strictly on a division of movement into these two right-angle

planes. It may be attained by a blending of the two and may occur as the manus rotates one way or the other around the lower-limb axis.

The sauropod carpus and its function are poorly known, but the number of bones

involved is a small fraction of the number found in titanotheres and elephant carpi, supporting a long-held conviction (Hatcher 1901) that sauropod locomotion was little more than slow and ponderous and cannot realistically be modeled on the physical activities of modern, large mammals.

JOINT SURFACES.—Bone ends forming sauropod limb and foot joints are of simple geometric form, compared with the geometrically sophisticated joint design in mammals, in which all apposing spherical and curvate surfaces are precisely matched as male and female systems (Figs. 10B–C, 11B–F₄, 12B–D). The irregular, spongy, rugose surfaces (Figs. 10A₁, A₂) forming sauropod joint areas attached cartilaginous articulating structures of unknown form, none of which have been found as ossified elements. These thick, cartilaginous pads (Hatcher 1901) were probably composed of varying tissue densities and certainly lacked the rigidity and structural resistance to deformation of the close-fitting, compact joints seen in the integrated geometrical shapes of mammalian joints (Figs. 10–12). This inherent joint weakness in sauropods was a limiting factor and is a reality that must be included in all qualitative comparisons of sauropod and mammal locomotion and other physical behaviors. Such studies will reveal the comparative ineffectiveness of the sauropod joint system, and all speculations regarding the comparative physical abilities of mammals and sauropods must be tempered by this biomechanical reality. Furthermore, because of the high-energy demands of running, speculations about sauropod metabolic tempo and the vulgar term “hot-bloodedness” might also be examined from a strictly mechanical point of view inasmuch as the sauropod skeleton, being a mechanical arrangement, was not designed to move rapidly; its great weight, simple limb and foot joint structure, and particularly the nonrigid, cartilaginous composition of the joints in its appendicular skeleton all argue strongly against its being able to run, or move about bipedally, even if it possessed a high metabolic rate.

The geometric shape of any joint controls its mechanical function, and, though the force of gravity is mitigated when a body floats in water, a joint's movement and excursions limits are constant despite the presence or absence of gravity. Although sauropod limb joints

were constructed of nonossified cartilaginous tissue, they were nevertheless restricted by their form to certain limits of excursion, while being required to support far greater weight per unit area of joint surface than that carried by equivalent joints in the elephant and titanotheres. A sauropod's cartilaginous joint structure was obviously adequate for walking gaits, during which there was an alternate shifting of many tons of body weight from the joints of one leg to those of another. But if the gait were to be accelerated from walking to running, the joints would probably be subjected to a disproportionate increase in impact stress, creating a danger of joint failure and pathological bone fracture.

Ten years of work experience as a longshoreman on the waterfront, operating cranes and lifts handling more than 50-ton loads, has convinced me that the notion of a single, cartilaginous sauropod ankle joint capable of momentarily carrying a 40-ton, or even supporting a 20-ton, static load is structurally impossible. However, *C. lewisi* appears to have successfully functioned bipedally because of its various structural specializations; but, judging from its body size and the mature condition of fused epiphyseal unions present in the articulated skeleton of the type-specimen, it was a small sauropod of probably no more than 10 to 15 tons.

An elephant's weight is but a fraction of that of a large sauropod, and yet, despite its ball-and-socket acetabular joints, the elephant moves ponderously in bipedal activity. Any departure from quadrupedal locomotion by sauropods weighing more than 10 times as much as an elephant would have been very difficult and vastly more ponderous, if not impossible. No sauropod could raise its multi-ton body to a vertical position without the mechanical and muscular adaptations necessary to pay the weight tax imposed by gravity. The stresses of weight, friction, pressure, and inertia, imposed by gravity today, applied equally to Jurassic animals on a planet of essentially the same diameter and density.

TRIAD BONES.—Two different elements, sesamoids (Fig. 10F) and patellae (Fig. 10C), are present in the locomotor apparatus of mammals, and each type functioned in a triad joint. These two elements were absent from sauropod limbs and feet, which had no triad joints.

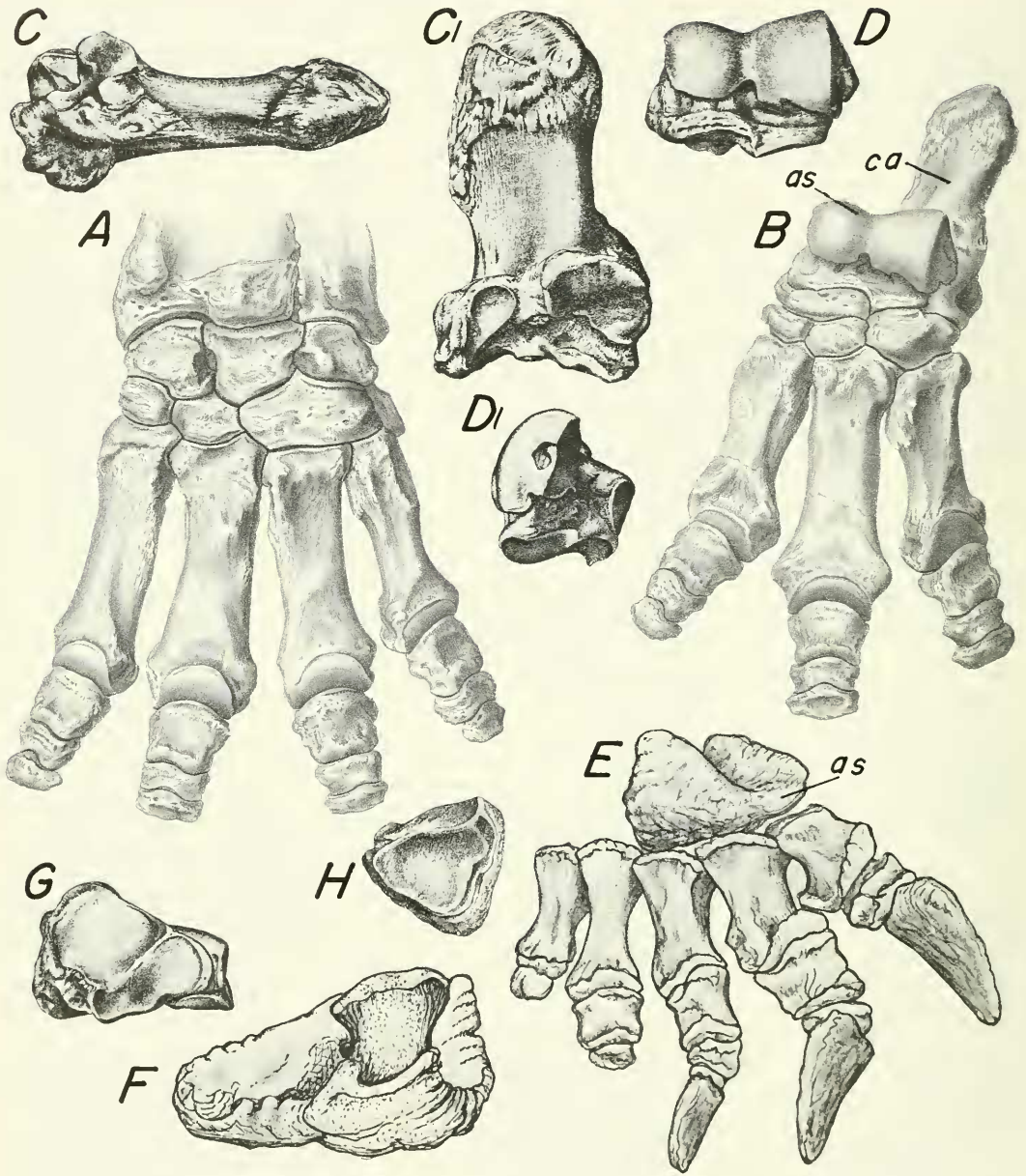


Fig. 12. Mammal, Brontotheridae, A-D₁, G; sauropod dinosaurs, Camarasauridae, E-F. Mammal, *Brontops*: A, left manus; B, left pes; C, left calcaneum, external view; C₁, anterosuperior view; D, left astragalus, anterior view; D₁, lateral view. Dinosaurs: *Apatosaurus*, E, right pes and astragalus; *Camarasaurus*, F, left astragalus. Abbreviations: as—astragalus; ca—calcaneum. Not to scale.

I submit that the function and importance of these two bone types in the mammalian locomotor apparatus indicate a significant difference between the mammalian physiological system and that of a sauropod by implying a discrepancy between two levels of physical activity, and that a discussion of the nature

and importance of that difference is relevant to a consideration of the well-known proposition that *sauropods were capable of little more than slow, ponderous locomotion* (Colbert 1961).

SESAMOID BONES.—Sesamoid bones are imbedded in the plantar surface of all four feet

in mammals, each sesamoid forming a triadal union with two apposing phalangeal elements by articulating with the ventral surface of their joints. The distal, ventral surfaces of the metatarsal and metacarpal bones, and the ventral surface of the digital joints move in conjunction with the superior articular surfaces of the sesamoids, the entire triad joint system being encapsulated with lubricating fluid. Sauropod feet lacked sesamoid bones and triadal joints.

Sesamoid articular surface area was no doubt greatly enlarged by dense cartilage formed around the bone, similar to the cartilaginous enlargement of the articular surface in the avian patella (Numididae, Meleagrididae, personal experience). This cartilaginous enlargement of sesamoid bone would have increased ventral support from the sesamoid bone to the triad joint, probably by 100%. The majority of phalangeal joints in mammalian feet are triadal.

Variable pressure from body weight, fluctuating according to the intensity of foot activity, is exerted on the phalanges by various muscles, such as the *M. flexor profundus digitorum* and surrounding adductive tissues. This pressure is transmitted through the lubricated triadal joint and into the substrate by the inferior position of the sesamoid bone, mitigating (to an unknown degree) the effects of friction from flexure within the massive footpad tissues. Sesamoid bones also protect the ventral surfaces of phalangeal joints from damage during the radical flexure of vigorous activity. If the footpad were peeled away from the plantar, or ventral surface of the phalanges, the superior surface of the footpad would display the lubricated joint surfaces of the sesamoid bones remaining imbedded in footpad tissue. Sauropod metatarsi and metacarpi had no such intermediate bony structures supporting their ventral surfaces and transmitting weight to the substrate on which the foot rested.

It has been suggested, based on an incomplete, partially disarticulated sauropod pes (Gilmore 1923), that sesamoid bones may occur in sauropod feet; however, in more recent years I collected an articulated lower leg and complete pes of a Jurassic camarasaurid (Figs. 7A–C) that clearly revealed the few small "sesamoid" bones of Gilmore to be very compressed distal phalanges, which, with

greatly shortened axes, resemble mammalian sesamoid bones.

Sesamoid bones in mammalian feet aid in the distribution of weight and pressure and the reduction of intraphalangeal friction, by presenting a lubricated surface, imbedded in plantar cartilage, over which the ventral surfaces of the phalanges move, enabling large mammals to engage in accelerated activities and lighter ones, such as the cheetah, to move at high speeds.

PATELLA.—In the titanotheres *Palaeosyops* (Osborn 1929) the patella is involved in both flexing and extending the rear limb. The *M. rectus femoris*, one of the major femoral flexors, inserts the proximal end of the patella. The principal extensor muscles, the *M. biceps 3* complex, insert in serial fashion down along the broad aponeurosis of insertion, anchoring the patella to the proximal end of the tibia. This complex, together with the *M. semi tendinosus-1* and *M. semi membranosus*, constitutes a powerful muscular force at the knee, extending the titanotheres rear limb (Osborn 1929). During fast locomotion the patella, as a muscular junction across the knee joint, provides a continuously effective distribution of muscular force against both ends of the apposing limb bones involved, the femur and tibia. No evidence exists for equivalent muscular energy, applied simultaneously to femur and tibia, to extend the sauropod rear limb. Muscles extending its rear limbs were comparatively weak, having a much smaller ratio of muscular leverage to total limb length than the ratio seen in titanotheres. Sauropod femoral extensors inserted on the fourth trochanter, generally located scarcely halfway down the femoral shaft, whereas in titanotheres (Osborn 1929) rear limb extensors originated high on the neural spines and pelvis and insert at, and below, the total length of the femur.

The patella remains near the head of the tibia during locomotion, being attached there by the broad aponeurosis of insertion carrying various rear limb extensors. These muscles, including the *M. biceps 3* complex, contact the aponeurosis of insertion in an extended dorsoventral area spanning the femorotibial joint. When the knee is flexed, the posteroproximal surface of the patella moves in a radial path over the anterodistal joint surface of the femur, regardless of the varying

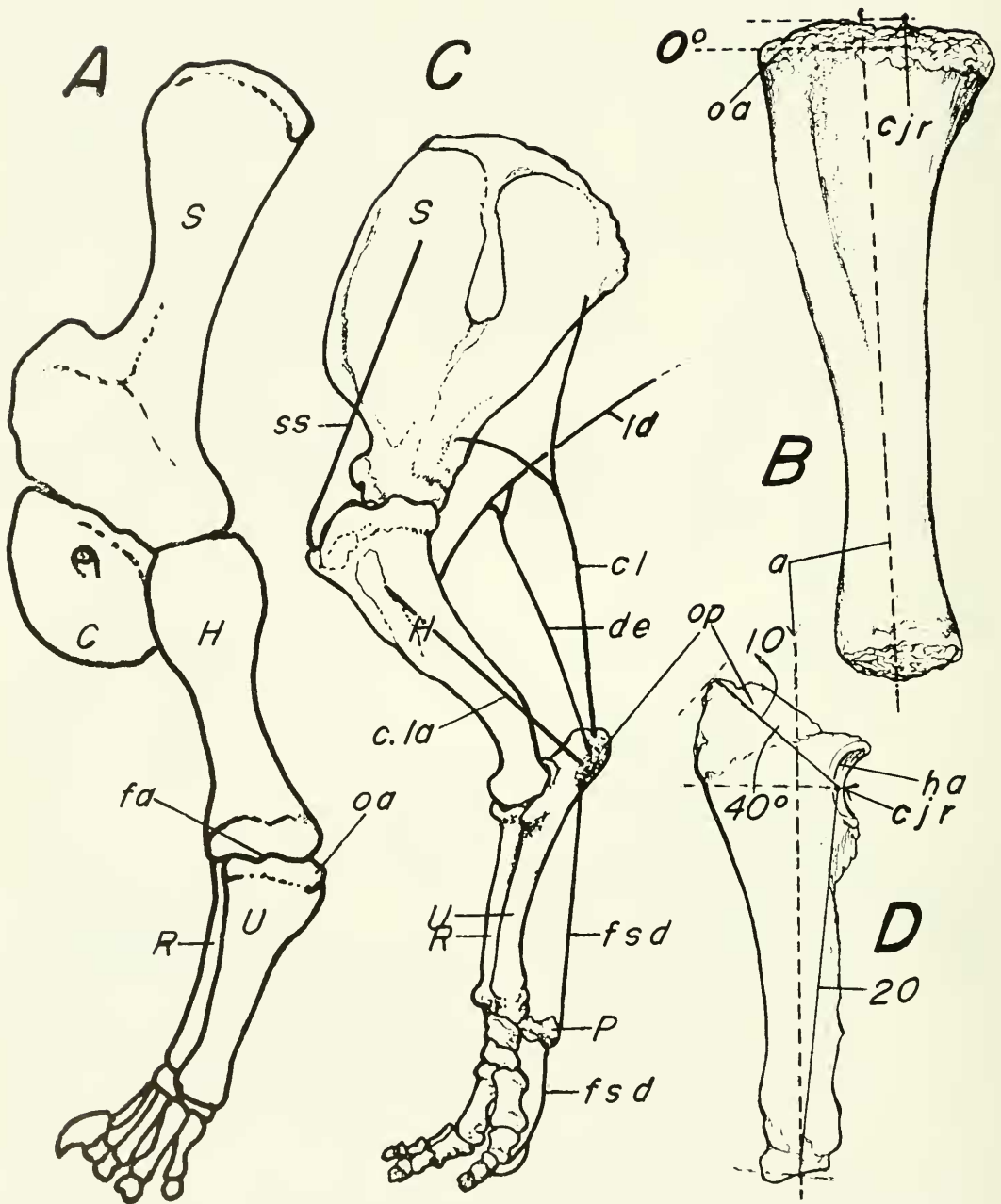


Fig. 13. Dinosaur and mammal forelimbs: A, the sauropod *Camarasaurus* forelimb; B, camarasaur ulna; C, titanotheres forelimb; D, titanotheres ulna. Abbreviations: C—coracoid; H—humerus; P—pisiform; R—radius; S—scapula; U—ulna; a—axes; cjr—center of joint radius; c.la—M. caput laterale; el—M. caput longum; de—M. dorso-epitrochlearis; fsd—M. flexor sublimis digitorum; ha—humeral articulation; ld—M. latissimus dorsi; oa—olecranon area; op—olecranon process; ss—M. supra spinatus; 40 degrees = height of olecranon process above center of joint radius; 10 = leverage factor of olecranon process on humeral articulation and against ulnar shaft length; 20 = ratio of 2:1. Not to scale.

angularity developed between the axes of femur and tibia, transmitting rectilinear force across the working joint.

The superiority of titanotheres rear limb function and power over that of sauropods is demonstrated by the length of the M. biceps 3

group and the participating *M. gluteus maximus*, *M. semi membranosus*, and *M. semi tendinosus*-1, all of which extend from elevated origins on the sacral spines, caudal vertebrae, and posterior pelvis to the aponeurosis of insertion attaching the patella to the tibia. As noted, these muscles exert a powerful extending force at the *middle* of the rear limb, whereas sauropod rear limb extensors have comparatively weak muscular leverage, inserting as they do on the fourth trochanter approximately halfway down the femoral shaft. This comparison demonstrates the superior ability for fast locomotion in mammals. Patellar function appears to be essentially the same in all mammals. The posterior surface of the patella, with a rounded dorsoventral, median ridge (Fig. 10C), is almost entirely occupied with knee joint function in a lubricated environment.

Judging from rear limb attitudes seen on various mounted sauropod skeletons in North American museums (some mounts appearing more realistic than others), the femorotibial angle of flexure in a sauropod's lower leg was small, with the angle rarely exceeding 45 degrees.

Because of their great weight and unsophisticated limb and foot joint structure (Figs. 7B-C), I am convinced that sauropods were slow-moving creatures with a moderate to low rate of catabolic metabolism; that is, they were homeothermic but not endothermic. As slow-moving animals, the sauropods were able to function without the complex joint geometry of mammals; but their great weight and cartilaginous joint structure, lacking patellae and sesamoid bones, made it difficult, if not impossible, for them to run, which would have required an accelerated metabolic rate.

I believe, in view of its structural and apparent soft-tissue development, that *C. lewisi* habitually assumed a bipedal posture and did so without patellae and sesamoids but, except for localized shifts in feeding positions, that its general locomotion probably remained a quadrupedal event.

OCCURRENCE AND TAPHONOMY

Dominguez/Jones Quarry is located on the eastern monocline of the Uncompahgre Uplift in Mesa County, Colorado, and consists

of two pits 300 m apart on approximately the same horizon, 10 m above the base of the Brushy Basin Member of the Morrison Formation. Each pit produced remains of a single sauropod, the nearly complete skeleton of *C. lewisi* coming from Pit 1 and the pelvis, some rear limb material, and most of the caudal vertebrae of a second unknown sauropod (to be described elsewhere) being collected from Pit 2. Both occurrences were autochthonous. The skeletons were buried near their death site in well-graded (now), pale green sediments in a relatively quiet depositional environment an unknown distance from intermittent levee overwash during burial.

When *C. lewisi* was discovered, the axis of its vertebral column was crescentically distorted (Fig. 1E), with the tail and neck dorsally curved toward each other, the two curves oriented downstream toward each other, confluent with an apparent NE stream flow. This direction of hydraulic pressure was later verified by the position of disarticulated front limb elements (Figs. 1D, F) transported beyond the carcass before final burial.

No lenticular sandstones or other high-energy structures were present adjacent to the skeleton, or nearby on the same horizon, although some postmortem disturbance was evident in the displacement of front limb elements several meters downstream from the carcass (Figs. 1D-F). Deep teeth marks in the left ilium (Figs. 3C, 4C-C₁) and the final disposition of the skeleton (Figs. 1D-F) suggest that a large carnivore, equal in size to *Torvosaurus tanneri* Galton & Jensen (1979), killed and fed on the sauropod. Apparently the body was turned over later and dismembered during a second feeding by the killer or another predator of equal size, providing one explanation for the absence of rear limb and foot elements. The neck and rib cage were preserved intact, indicating predator preference for the more heavily muscled pelvic-rear limb area as the best food source. Between the large carnosaur(s) feeding periods, small scavenging carnosaurs intruded and fed, imposing their teeth marks across the much larger tooth marks in the ilium.

An unknown period of time after the kill and initial feeding invasion, during which the killer fed only in the rear limb and pelvic area, an overbank flood may have floated the bloated carcass an unknown distance from the

death site and initial feeding episode, further explaining the absence of rear limb elements near the skeleton. Small, eroded, organic detritus, common in allochthonous deposits, was entirely absent from matrix surrounding the skeleton.

When the skeleton of *C. lewisi* was collected in 1967, the existence in the Uncompahgre fauna (Jensen 1985) of a sauropod killer more powerful than *Allosaurus* was deduced from the size and spacing of teeth marks in the ilium (Fig. 5A), but the first elements of such a carnosaur, later described as *Torvosaurus tanneri*, were not discovered until five years later in Dry Mesa Quarry. The many elements known from this new carnosaurian genus (Jensen 1985) indicate an animal large enough to easily catch, kill, and dismember a sauropod the size of the *C. lewisi* skeleton; however, various elements of an unusually large allosaurid (to be described elsewhere) were subsequently found in Dry Mesa Quarry and represent an individual also capable of easily killing medium-sized sauropods.

ACKNOWLEDGMENTS

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MEMORIAL

A tribute is paid to the late Daniel E. "Eddie" Jones, of Delta, Colorado, on behalf of the discipline of Vertebrate Paleontology and in particular all workers and students interested in dinosaurs. All will be forever indebted to his many years of successful efforts to find dinosaurs in Colorado.

"Eddie," with his wife, Vivian, as his con-

stant companion, over a period of more than 20 years made the greatest single contribution to the renewal of dinosaur studies occurring in the last half century. Because of the productive localities they discovered and revealed to science, an important new group of fossil vertebrates was uncovered, including the "world's largest" dinosaurs and a new flying reptile. These discoveries received wide international media exposure, catapulting many eager, young minds into the beginning flush of a great "dinosaur renaissance." Elementary school children, excited over new dinosaurs from the Jones's discoveries in the 60s, are now professional vertebrate paleontologists, judging from my 25-year accumulation of thousands of letters.

"Eddie" and Vivian's persistent toil over many rough mountain ridges and exhausting, hot, dry badlands will continue to pay scientific dividends for many years of dinosaur research in the future, while thousands of bones in localities they discovered still remain to be collected and studied. In 1985 two new sauropod dinosaurs were named in their honor: *Dystylosaurus edwini*, and *Supersaurus vivianae*. Thank you, "Eddie."

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